

Phallus morphology in caecilians (Amphibia, Gymnophiona) and its systematic utility

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SYNOPSIS. The cloaca of male caecilian amphibians (Gymnophiona) is a tube that comprises an anterior urodeum and a posterior phallodeum. The phallodeum everts (with the urodeum lying inside it) to form a phallus used for direct sperm transfer in copulation. Phallodeal morphology is rich in detail and variation, and has therefore been considered a potentially useful and much needed tool for caecilian phylogenetics and species-level taxonomy. Despite this, it has been almost entirely ignored in caecilian systematics, there is confusion regarding some aspects of morphology, and variation within and among species is poorly understood. A short review and reconsideration of phallus morphology is presented, and the systematic potential assessed. The anterior part of the phallodeum appears to offer the most obvious systematic potential, and the morphology of longitudinal ridges and their ornamentation here seem to have diagnostic and/or phylogenetic value for some taxa. Although there is evidence of intraspecific variation, at least some of which is associated with ontogeny and reproductive condition, individuals of the same species generally have a common pattern of phallodeal ridges and ornamentation, and congeners often share a similar pattern. However, these patterns are not universally species specific, at least among uraeotyphlids. Although variation needs to be better understood, the male cloaca offers great potential for caecilian systematics.

INTRODUCTION

As in other amphibians, caecilians (Gymnophiona) possess a cloaca, a chamber that opens to the exterior via the vent and into which open the large intestine, the urogenital (Wolffian and Müllerian) ducts, and the bladder. In contrast to other amphibians, the cloaca of male caecilians can be everted through the vent (Fig. 1) to serve as an intromittant organ, or phallus, used in copulation to effect direct sperm transfer (e.g. Himstedt, 1996). It has long been recognised that the external surface of the caecilian phallus and the corresponding internal surface of the uneverted cloaca may bear distinctive ridges and grooves, tuberosities and even spines (e.g. Duvernoy, 1849; Günther, 1864; Spengel, 1876; Noble, 1931). There is considerable interspecific variation in the complex patterns of these features, but there have been few comparative studies.

Spengel (1876) compared cloacal features in males of six species in what are now recognised as six genera from three families, and aspects of cloacal morphology were compared further in some of these species by Wiedersheim (1879). Tonutti (1931) provided a very detailed documentation of the uneverted and everted cloaca of the caeciliid *Hypogeophis rostratus* (Cuvier, 1829) and compared it with the uneverted cloaca of the ichthyophiid *Ichthyophis glutinosus* (Linnaeus, 1758) and of the caeciliid *Spiononops annulatus* (Mikan, 1820). Tonutti (1933) expanded the comparative aspect of his study of the caecilian phallus by incorporating detailed data on a further six species, including representatives of Scolecomorphidae and Typhlonectidae. Tonutti's work remains the most detailed to date. Taylor (1968 and references therein) figured (though without labels or orientation) everted phallodea and *in situ* dissections of 12 species in eight genera and four families. The broadest comparative study of the male cloaca was presented by Wake (1972), who examined

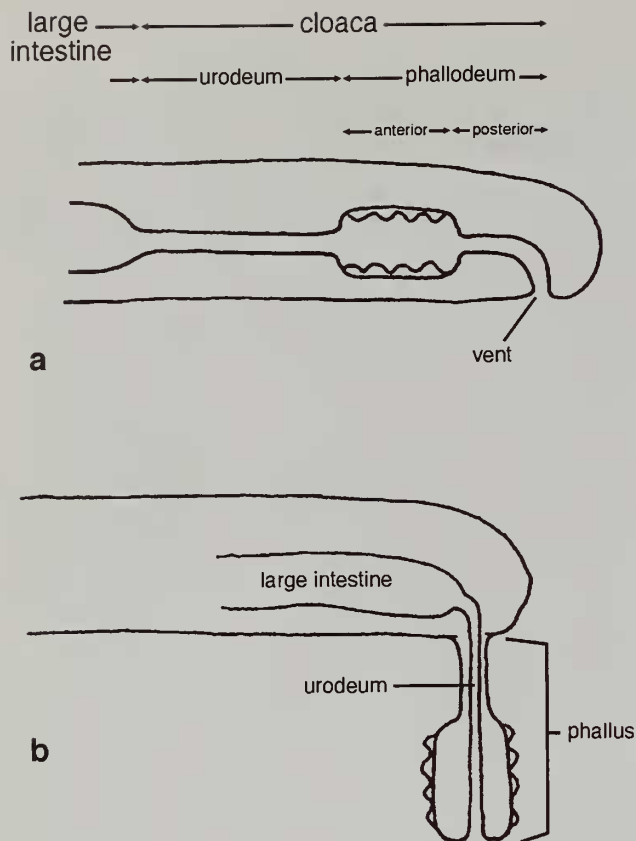


Fig. 1 Schematic sagittal section through the posterior of a male caecilian showing (a) main divisions of the unverted cloaca, and (b) the everted phallus with the internal, luminal surface of the phallodeum on its exterior surface, and the urodeum forming its core.

34 caecilian species, including representatives of 20 currently recognised genera and all six of the currently recognised families. Exbrayat (1991) compared cloacae of single species from four genera in three families. Wake (1998) provided comparative data on the cloacal spines and spicules of the three nominate species of *Scolecophorus* Boulenger, 1883.

Species limits in caecilians are poorly understood and the taxonomy within many genera is best viewed as uncertain and potentially unstable (Nussbaum and Wilkinson, 1989). The inadequate state of current knowledge has been attributed to the group's tropical distribution, largely fossorial and secretive lifestyle, under-representation in museum collections, lack of detailed study, and a relative paucity of obvious external morphological features in association with their limbless bodies, reduced or absent tails, and reduced head features (e.g. Nussbaum & Wilkinson, 1989). Some 34 years after the publication of Taylor's (1968) taxonomic monograph, species level caecilian systematics is still dominated by counts of annuli, vertebrae, and teeth. Of the phallus, Taylor (1968: 31) was 'certain that most genera and many species could be identified by the characters of this organ alone' and Wake (1972: 353) stated that 'the arrangement of musculature and cloacal accessory structures is species-specific in males.' If correct, male cloacal morphology, with its complex structure and many variations, should provide a much needed tool for investigating species limits in and phylogenetic relationships among caecilians. However, not much has changed since Largen *et al.* (1972: 187) pointed out that 'The value of penis structure as a taxonomic character has yet to be fully investigated'.

We have made observations of the cloacal morphology of a broad range of caecilian species. Without assembling a thorough synthesis of these observations, we draw upon them here to provide a description of the male cloaca that emphasises some features that can be homologised across taxa, and that indicates the kind of variation that occurs. It is hoped that this contribution will clarify some points of confusion in the literature and be a stimulus to future research. Our focus here is on the male cloaca only.

Abbreviations

Text

UMMZ: University of Michigan, Museum of Zoology.

Figures

a.ll	anterior tuberosity of l.l
a.md	anterior tuberosity of md
ap	anterior part of phallodeum
a.rdl	anterior tuberosity of r.dl
a.rvl	anterior tuberosity of r.vl
b	bladder
bp	blind pit
bs	blind sac
c	colliculus
cl	copulator loop
c.md	central tuberosity of md
cs	cloacal sheath
ebs	entrance to blind sac
eu	entrance to urodeum
i	intestine
l.bs	left blind sac
l.dl	left dorsolateral longitudinal ridge
l.l	left lateral longitudinal ridge
l.vl	left ventrolateral longitudinal ridge
md	mid-dorsal longitudinal ridge
p	phallodeum
p.lvl	posterior tuberosity of l.vl
p.md	posterior tuberosity of md
pp	posterior part of phallodeum
p.rdl	posterior tuberosity of r.dl
p.rl	posterior tuberosity of r.l
p.rvl	posterior tuberosity of r.vl
r.bs	right blind sac
r.dl	right dorsolateral longitudinal ridge
r.l	right lateral longitudinal ridge
rm	retractor muscle
r.vl	right ventrolateral longitudinal ridge
s	sulcus
sph	sphincter
u	urodeum
ud	urogenital duct
umd	mid-dorsal ridge of urodeum
v	small additional ventral tuberosity
vd	vent denticulations
vp	vascular plexus

MORPHOLOGY

DISPOSITION OF THE CLOACA. The cloaca of male caecilians is essentially a tube that extends between the posterior end of the intestines and the vent, and that may or may not have paired dorsal diverticula or blind sacs. The intestines, the paired urogenital ducts

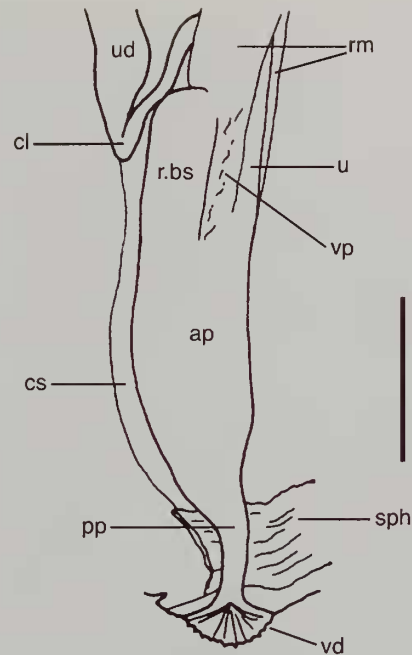


Fig. 2 *Uraeotyphlus* cf. *narayani* (field tag MW 249). Phallodeal portion of undissected, unevverted cloaca exposed in the coelom by a mid-ventral incision through the body wall. The phallodeum has been rotated about its long axis through 90° to show its right lateral aspect. Scale on drawing = 5 mm.

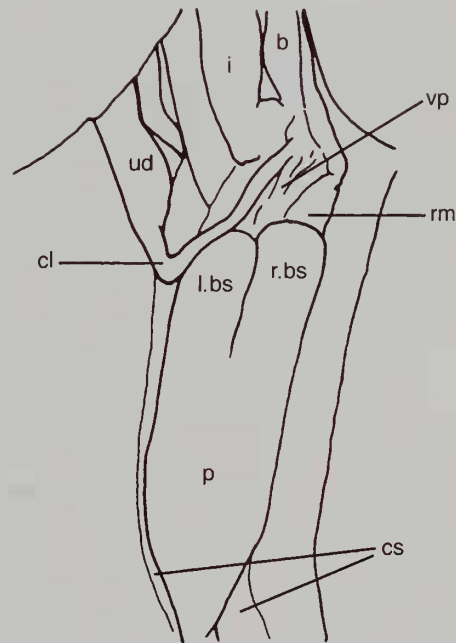


Fig. 3 *Uraeotyphlus* cf. *narayani* (field tag MW 249). Anterior phallodeal portion of undissected, unevverted cloaca exposed in the coelom by a mid-ventral incision through the body wall. The phallodeum has been rotated about its long axis through 180° to show its dorsal aspect. See Fig. 2 for scale.

and bladder open, in close proximity, into the cloaca at its anterior end. The openings of the ducts and bladder are in the dorsolateral and ventral wall of the cloaca respectively. The Müllerian and Wolffian ducts and the intestine may extend posterior to their points of entry into the urodeum before turning back on themselves in U-bends or copulator loops that facilitate the eversion of the phallus

(Duvernoy, 1849; Günther, 1864; Spengel, 1876; Sawaya, 1942; Wilkinson, 1990; this paper: Figs. 2, 3). As documented by, for example, Rathke (1852), Günther (1864), Spengel (1876), Wiedersheim (1879: 89, Fig. 89) and Tonutti (1931, 1933: e.g. Fig. 32), the mature male cloaca sits within a membranous cloacal sheath, to which it is unattached other than at its anterior and

posterior ends (e.g. Rathke, 1852; Tonutti, 1931; Exbrayat, 1996). This loose association presumably also facilitates cloacal eversion (e.g. Spengel, 1876; Wilkinson, 1990). The sheath is continuous with the mesorchium and with the parietal peritoneum via a ventral mesentery (e.g. Tonutti, 1933; Fig. 3a).

A *musculus retractor cloacae* that is unique to caecilians originates on the mid-ventral body wall and inserts posterior to its origin on the lateral and ventral surface of the cloaca. In those taxa possessing blind sacs, the insertion is bifid and is largely or perhaps entirely on the sacs themselves (e.g. *Ichthyophis* Fitzinger, 1826 Tonutti, 1931; Fig. 30e; pers. obs.; *Uraeotyphlus* Peters, 1879, this paper: Figs. 2, 3). This muscle is thought to retract the everted phallodeum when contracted (e.g. Günther, 1864; Spengel, 1876).

DIVISIONS OF THE CLOACA. The cloaca can be divided along its long axis into two main regions (e.g. Duvernoy, 1849; Tonutti, 1931) – an anterior cloacal chamber, or urodeum, and a posterior cloacal chamber, or phallodeum (Fig. 1). The phallodeum of mature individuals is also broadly divisible into two regions, an anterior part with pronounced ornamentation that forms the more distal part of the everted phallus, and a structurally more simple posterior section that forms the proximal stalk of the everted phallus. Günther (1864) and Wiedersheim (1879) discussed three regions in the male cloaca. Their anterior region corresponds to the urodeum, and their middle and posterior parts correspond to the anterior and posterior sections of the phallodeum, respectively. Exbrayat (1991) also distinguished three regions of the cloaca, but these do not correspond directly to the partitions recognised by other authors. His middle section includes the posterior part of the urodeum and the anterior phallodeum.

The most obvious variations in cloacal morphology occur on the internal, luminal surface of the phallodeum, which corresponds to the external surface of the phallus. The morphology of this surface can be examined directly in caecilians preserved with the phallus fully everted, or by dissection, serial sectioning or endoscopy (Himstedt, 1996). Comparison of dissected cloacae is best effected by maintaining an approximately standard approach. Figures of dissected cloacae in the literature (e.g. Duvernoy, 1849; Günther, 1864; Spengel, 1876; Taylor, 1968; Wake, 1972; this paper) are mostly of cloacae opened with a longitudinal mid-ventral incision. This procedure gives a clear view of the dorsal surface of the phallodeum. Features of the urodeum must be determined by dissection, sectioning, or endoscopy. The caecilian phallus is sometimes referred to as the phallodeum (e.g. Duellman & Trueb, 1986), but the latter term is more properly reserved for the posterior cloacal chamber. The urodeum, at least in part, also contributes to the phallus by forming its core as it lies inside the everted phallodeum (e.g. Tonutti, 1931; Fig. 22b; this paper: Fig. 1).

In the majority of caecilians, the distinction internally between the urodeum and phallodeum is obvious in dissected specimens. The relatively simple and narrow urodeum gives way posteriorly to the broader phallodeum, which has pronounced longitudinal (and/or oblique) ridges and deep sulci extending to the phallodeal-urodeal border (e.g. see figures of *Uraeotyphlus* below). In most taxa, a mid-dorsal protuberance marks the posterior end of the urodeum. This protuberance is here termed *colliculus* (=little hill). The colliculus is perhaps equivalent, at least in part, to the 'bourrelet' mentioned by Duvernoy (1849; also Exbrayat, 1991). Typically the colliculus projects into the phallodeal chamber to a varying degree, being particularly large in some species (e.g. pers. obs. of *Gegeneophis ramswamii* Taylor, 1942, *Herpele squalostoma* (Stutchbury, 1834), and *Microcaecilia unicolor* (Duméril, 1864)). In species with blind sacs, these open into the phallodeum adjacent to its border with the

urodeum. A major exception to this general pattern is apparently restricted to the caeciliid genera *Dermophis* Peters, 1879 and *Gymnopsis* Peters, 1874 (MW, pers. obs.). In these caecilians, which lack blind sacs, there is no definite colliculus and no clear differentiation between urodeum and phallodeum. Given the apparently universal presence of distinct phallodeal and urodeal chambers in all other caecilians, including all non-caeciliids (outgroups), we interpret its absence as a putative synapomorphy of *Dermophis* and *Gymnopsis*.

Wake (1972) made no use of a clear urodeum-phallodeum division in her descriptions. She documented several features close to the openings of the urogenital ducts, which are in the anterior urodeum rather than the phallodeum. In our experience, this is a far more irregular region in which gross morphological regularities are less apparent and variation is harder to characterise than in the phallodeum. Wake (1972) mostly examined partially opened cloacae in which only the anterior part of the phallodeum could be observed.

The absolute and relative sizes of the urodeum and phallodeum may vary taxonomically but substantial variation within species might be expected given that the cloaca must serve both reproductive and alimentary functions. Exbrayat (1991) has presented evidence of seasonal variation correlated with the breeding cycle in *Typhlonectes compressicauda* (Duméril and Bibron, 1841), and short term changes might even occur with the passage of faeces. In a sample of 11 preserved *Hypogeophis rostratus*, the phallodeum ranged from 1.6 to 5.3 times the length of the urodeum (MW, pers. obs.), demonstrating considerable intraspecific variation in size in this species.

URODEUM. The urodeum is a relatively simple and typically narrow chamber. Its dorsal surface is characterised by a pronounced mid-dorsal longitudinal ridge (see figures of *Uraeotyphlus* below) and seemingly irregular arrangements of other, less pronounced ridges. The appearance of the lesser ridges can vary substantially with state of preservation and possibly also in life. The colliculus is an expansion of the posteriormost part of the mid-dorsal urodeal ridge, and it shows variations in form that may be of systematic value, as may differences in the overall shape of the urodeum (long and narrow or short and somewhat broader). Additional lateral or ventral more pronounced longitudinal ridges may also be present in the urodeum (Wake, 1972). Wake (1972) described considerable variation in the form of the urodeum at the points of entry of the urogenital ducts, which are often depressed and may vary in their relations to the mid-dorsal longitudinal ridge. She reported that papillae associated with the openings of the urogenital ducts were present only the typhlonectids (*Typhlonectes compressicauda*, *Chthonerpeton indistinctum* (Reinhardt and Lütken, 1861) and *C. viviparum* Parker and Wettstein, 1929) that she examined. However, one of us (MW) has observed urogenital papillae in other species, including taxa that Wake reported as lacking them (e.g. *Grandisonia sechellensis* (Boulenger, 1909) and *Geotrypetes seraphini* (Duméril, 1859)). Systematically useful variation may occur in the urodeum but we have not yet discerned clear patterns of variation.

BLIND SACS. Blind sacs (caecal appendage of Günther, 1864; Penisblindsack of Spengel, 1876; Blindsack of Wiedersheim, 1879; Penisack of Tonutti, 1931) are paired anterior extensions of the phallodeum that run parallel to the urodeum (Figs. 2, 3). Blind sacs vary in size and they may be free or partially fused to the adjacent urodeum (e.g. Wake, 1972). In species with blind sacs, these are a feature of the mature cloaca and may be absent or less well developed in immature males (see discussion of *Uraeotyphlus* below). In most cases, species within the same genus, or that are otherwise

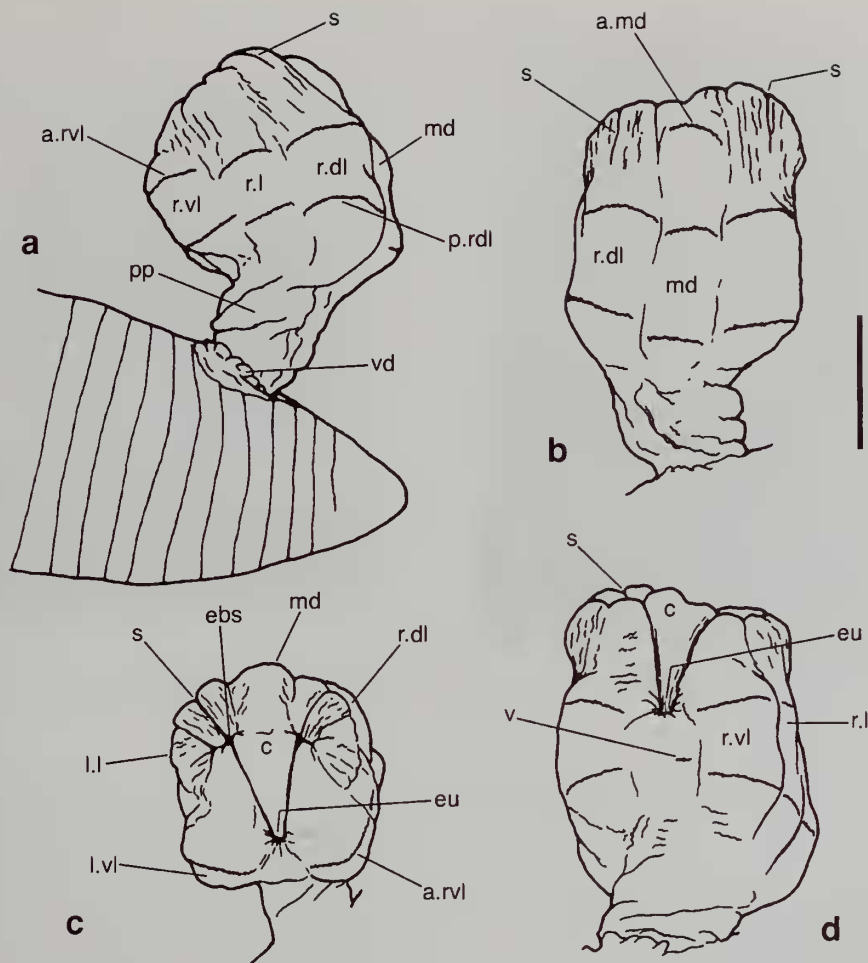


Fig. 4 *Uraeotyphlus* cf. *narayani* (field tag MW 207). Views of (a) right lateral, (b) dorsal, (c) distal and slightly ventral, and (d) ventral surfaces of phallus (everted cloaca). Scale bar for Fig. 4b = 3 mm.

considered to be closely related, have blind sacs in a similar condition, suggesting relatively stable and systematically informative interspecific variation. Blind sacs are well developed in ichthyophiids and uraeotyphlids, caecilians that Wake (1972) considered 'primitive' in other reproductive characters, leading her to suggest that well developed blind sacs are a general caecilian feature, with reduction and loss being derived. In contrast, Tonutti (1931, 1933) considered well developed blind sacs derived. Rhinatrematids are believed to be the sister group of other extant caecilians on the basis of a wide variety of evidence (e.g. Nussbaum, 1977; Hedges *et al.*, 1993; Wilkinson, 1996). Spengel (1876) and Wake (1972) documented blind sacs in the rhinatrematids *Rhinatrema bivittatum* (Cuvier, 1829) and *Epicrionops petersi* Taylor, 1968 respectively, but we note their absence (or minimal development) in mature *Epicrionops marmoratus* Taylor, 1968 (MW, pers. obs.). This suggests homoplasy and may complicate the interpretation of polarity.

ANTERIOR PHALLODEUM. The luminal surface of the anterior phallodeum bears the distinctive structures seen on the external surface of the more distal part of the fully everted phallus (Figs. 1, 4 to 9). Much variation occurs here, but we discern a presumably homologous pattern anteriorly that is common to almost all caecilians. In this region there is a pair of deep dorsolateral grooves, one on either side. Each of these sulci (Figs. 4 to 9) are bordered by a pair

of well developed, parallel dorsolateral longitudinal or oblique ridges. A median mid-dorsal longitudinal ridge may or may not also be present, a variation that appears to be species specific. In species with blind sacs, the sulci and their bordering ridges run into the blind sacs, extending to their distal tips. In species lacking blind sacs, the ridges fade out and the sulci open out at the anterior of the phallodeum, either side of the colliculus. In *Hypogeophis rostratus*, the sulci run posteriorly and terminate blindly with the fusion of their associated ridges (Tonutti, 1931: Fig. 20; pers. obs.), a pattern that is consistent in the 11 specimens of this species examined by one of us (MW). Similar 'fusion' of the dorsolateral longitudinal ridges occurs in many caecilians (e.g. *Uraeotyphlus*, Figs. 6 to 9). Less commonly, the posterior end of each sulcus is open, with the more medial bordering ridge fading out or fusing with its antimerie along the dorsal midline (e.g. *Grandisonia alternans* (Stejneger, 1893), *Gegeneophis ramaswamii*, *Boulengerula boulengeri* Tornier, 1896, MW, pers. obs.). Additional major longitudinal ridges may or may not be present lateral and/or ventral to those forming the sulci. In uraeotyphlids (Figs. 4 to 9) and ichthyophiids, major longitudinal ridges are broadly distributed, whereas in some caeciliids (pers. obs. of e.g. *Grandisonia* Taylor, 1968 and *Schistometopum* Parker, 1941; this paper: Fig. 10) the ridges are more restricted to the dorsal surface of the phallodeum. Although we have discussed a single main pair of sulci, there may be other, smaller, more or less



Fig. 5 *Uraeotyphlus* cf. *narayani* (field tag MW 207). Views of (a) dorsal, and (b) distal and slightly ventral surfaces of phallus (everted cloaca). For scale see Fig. 4.

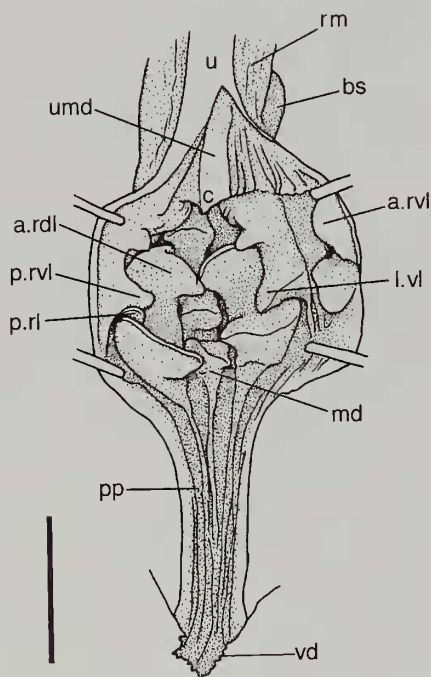


Fig. 6 *Uraeotyphlus* cf. *narayani* (field tag MW 254). Dissected cloaca of mature male. The cloaca has been opened mid-ventrally and pinned to reveal the luminal surface of the phallodeum and posterior part of the urodeum. The incision has longitudinally bisected the right ventrolateral longitudinal ridge so that parts of it lie on each side of the open cloaca. Scale = 3 mm.

longitudinal grooves at the anterior end of the phallodeum, at least some of which may enter the blind sacs, where present (e.g. *Geotrypetes* Peters, 1879, pers. obs.).

POSTERIOR PHALLODEUM. The distinction between the anterior and posterior phallodeum is sometimes less clear cut than that between the phallodeum and urodeum. Wake (1972) reported that the longitudinal ridges of the anterior phallodeum continue posteriorly to the vent. We find that the major longitudinal ridges reduce greatly posteriorly, either abruptly or gradually, that they may or may not extend as far as the vent, and that the pattern of ridges within the posterior phallodeum is irregular or less obviously regular than those of the anterior phallodeum. The phallodeum narrows dramatically posteriorly, shows considerable variation in length, and has its terminal portion surrounded by a sphincter of variable size.

PHALLODEAL ORNAMENTATION. The major longitudinal ridges of the anterior phallodeum may be more or less invested with, or elaborated into, tuberosities, transverse ridges and grooves, longitudinal crests, or spines that are often in distinctive patterns (e.g. Figs. 6, 9). Isolated thickenings or other ornaments may also occur in the spaces between the major longitudinal ridges. The ridges associated with the dorsolateral sulci bear such features only posterior to the sulci (e.g. Figs. 4, 7, 9). Both the shape and arrangement of this ornamentation may be expected to provide systematic characters, although there is also evidence of intraspecific variation (e.g. *Scolecormorphus*, Wake, 1998). Species appear to differ in whether the ridges within the posterior phallodeum bear any ornamentation or not. Where present, as in *Typhlonectes compressicauda* (Exbrayat 1996), they are not as pronounced or distinctive as the structures of the anterior phallodeum (distal phallus).

COMPOSITION OF PHALLODEAL STRUCTURES. The composition of the main longitudinal ridges and their ornamentation is unclear from

the literature and warrants further histological examination. Tonutti (1931, 1933) viewed the longitudinal ridges as encompassing longitudinal 'propulsor' muscles but we are unable to verify this from his figured sections. Wake (1972: 354) described the ridges as 'longitudinal muscles overlain by fibrous connective tissue', but also warned (p. 363) that 'Caution must be exercised in interpreting the various folds in the cloacal wall. They may often not be muscle but may be ridges of connective tissue'. Wake (1998) referred to connective tissue ridges in *Scolecormorphus* and made no mention of previous reports that ridges are muscular (Tonutti, 1933; Wake, 1972). Wake (1972) also referred to at least some phallosomal ornamentation as transverse muscle ridges, whereas Wiedersheim (1879) stated that the prominences are hardened parts of longitudinal folds of cloacal mucosa. In at least one case it is clear that the prominences are not muscular: large recurved calcified or cartilaginous spines are present in *Scolecormorphus uluguruensis* Barbour and Loveridge, 1925 (Noble, 1931; Taylor, 1968; Nussbaum, 1985; Wake, 1998). Exbrayat (1991) showed that tuberosities in the phallosome of *Typhlonectes compressicauda* are keratinous, and that their thickness varies with the reproductive cycle. Exbrayat (1996) described smooth transverse and striated longitudinal muscles in the wall of the cloaca of *T. compressicauda*, with the latter forming the major longitudinal ridges. Muscle therefore appears to be present in the longitudinal phallosomal ridges of at least some species, but we find no clear evidence that any of the tuberosities, crests etc found in the phallosome are muscular.

RELATIONSHIP BETWEEN THE UNEVERTED CLOACA AND THE PHALLUS.

There is some confusion in the literature regarding the positional relationship between structures as seen on the internal surface of the uneverted phallosome, and the same structures when observed on the external surface of the phallus. Wake (1972: 359, Fig. 13, 15) described and figured the blind sacs as being positioned at the proximal base of the everted phallus in a thickened 'blind sac sheath'. In the uneverted phallosome, blind sacs, where present, are pockets extending from the dorsal wall of the phallosome, very

close to the border between the phallosome and urodeum. The sacs extend anteriorly from the anterior end of the phallosome so that, within the coelom, they can be seen running parallel to the posterior end of the urodeum (e.g. Wiedersheim, 1879: Fig. 88; this paper: Figs. 2, 3). Thus, the blind sacs must be positioned at, or inside, the distal end of the everted phallus (Tonutti, 1931: e.g. Fig. 22b of *Hypogeophis rostratus*) rather than at its base. This can be clearly seen by comparing the figures shown here of the uneverted and everted phallosome of *Uraeotyphlus* (Figs. 2 to 9), where the entrance to the blind sacs are seen right at the distal termination of the everted phallus (Figs. 4, 5). Preserved specimens may show various degrees of phallosomal eversion, and it is clear that Wake's figures are of partially everted organs, which may have misled her. In our experience, the major dorsolateral sulci, their associated ridges, and the colliculus are clearly visible at the distal end of a well everted phallus, although the extent of phallosomal eversion during copulation is unknown.

Bons (1986) and Exbrayat (1991) also figured what we consider to be partially everted phallosomes of *Typhlonectes compressicauda*. *Typhlonectes* have a distinctive 'cloacal disc' surrounding the vent (Taylor, 1968) and Exbrayat's figure 3 appears to show the cloacal disk at the distal tip of the protruding phallus, and seemingly detached from the adjacent skin. However, the disc is continuous with the surrounding skin and must remain at the base of the phallus because it is everted rather than telescopically extended.

SYSTEMATICS

IS PHALLUS MORPHOLOGY SPECIES SPECIFIC? The family Uraeotyphlidae is monotypic, comprising five currently recognised species of *Uraeotyphlus* endemic to peninsular India (Pillai & Ravichandran, 1999). Uraeotyphlidae is the extant sister taxon of the south and southeast Asian Ichthyophiidae (Wilkinson & Nussbaum, 1996; Gower *et al.*, 2002; Wilkinson *et al.*, 2002). As

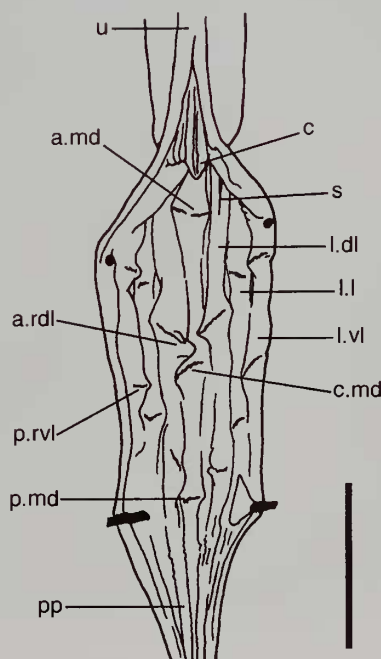
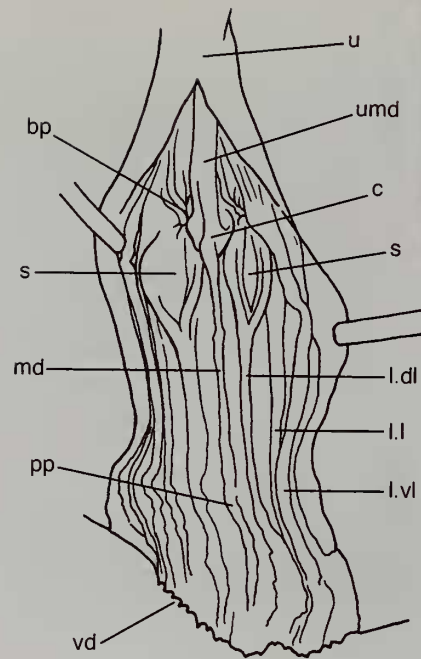


Fig. 7 *Uraeotyphlus* cf. *narayani* (field tag MW 172). Anterior phallosome of mature male, prepared as specimen shown in Fig. 6. Scale = 2 mm.



Fig. 8 *Uraeotyphlus* cf. *narayani* (UMMZ 139810). Cloaca of immature male, prepared as specimen shown in Fig. 6. Scale = 2 mm.



with many groups of caecilians, the taxonomy of *Uraeotyphlus* has an inadequate basis, with some species known from only few specimens, many with poor locality data. Few diagnostic characters have been identified and current keys are not satisfactory, so that caution needs to be exercised in applying names to individuals, and in assuming species identity of groups of individuals. The following discussion draws on the examination of the cloaca in more than 30 male *Uraeotyphlus* representing at least three distinct species. The focus here is on features of the luminal surface of the anterior portion of the phallodeum, chiefly the longitudinal ridges and their ornamentation.

Figures 4 to 8 show the morphology of the phallus and dissected cloacae of four specimens. These are identified as *Uraeotyphlus* cf. *narayani* Seshachar, 1939, but unpublished morphological and molecular data have revealed previously unsuspected diversity in the populations that these individuals are drawn from. It is not yet apparent whether this diversity is indicative of previously unrecognised specific or subspecific taxa. Whatever their true specific identity, these four specimens share a common pattern in the major features of the anterior phallodeum. There are seven major longitudinal phallosomal ridges – a single mid-dorsal ridge, and pairs of dorsolateral, lateral, and ventrolateral ridges. As in most other caecilians, the anterior end of each dorsolateral ridge holds a major longitudinal sulcus that extends into the corresponding blind sac (Figs. 4, 5, 9). In mature individuals, each of the major longitudinal ridges bear hardened transverse thickenings. When relatively small, these thickenings bear an approximately transverse narrow line of dense, opaque tissue that stands out against the more translucent main body of longitudinal ridge. Where relatively large, the thickenings are developed into tuberosities that can be irregular, and that interlock in the unverted cloaca. The mid-dorsal ridge bears three such tuberosities and the other, paired longitudinal ridges two each. The transverse thickenings of each major longitudinal ridge are offset relative to each adjacent ridge, and they generally bear the same spatial relationship to each other in each individual (Figs. 4 to 7). Of the paired ridges, the lateral ones are the least well developed,

and sometimes they are best located by their transverse thickenings. Within this common pattern are some minor variations. In immature males (Fig. 8), the main longitudinal ridges are less well developed and bear no transverse thickenings or indications of hardened tissue, but they can still be readily identified and homologised with those in mature males. In addition, the blind sacs of immature males are not developed. Instead, there is a pair of shallow pits in their place. The relative size of the transverse thickenings or tuberosities also varies

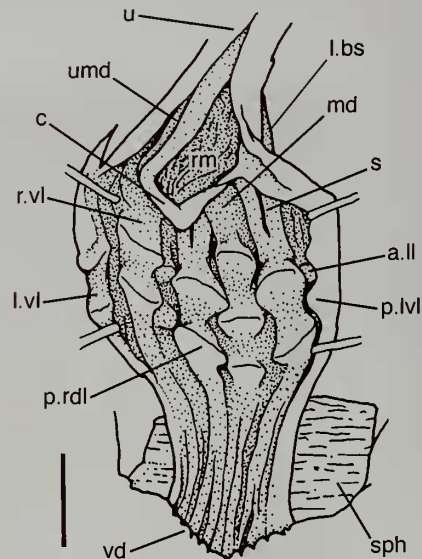


Fig. 9 *Uraeotyphlus* cf. *oxyurus* (field tag MW 469). Cloaca of mature male prepared as specimen shown in Fig. 6. The incision has longitudinally bisected the left ventrolateral longitudinal ridge so that parts of it lie on each side of the opened cloaca. The left side of the posterior end of the urodeum has been torn away from the anterior end of the phallodeum so that retractor muscle is visible through the resulting hole. Scale = 3 mm.

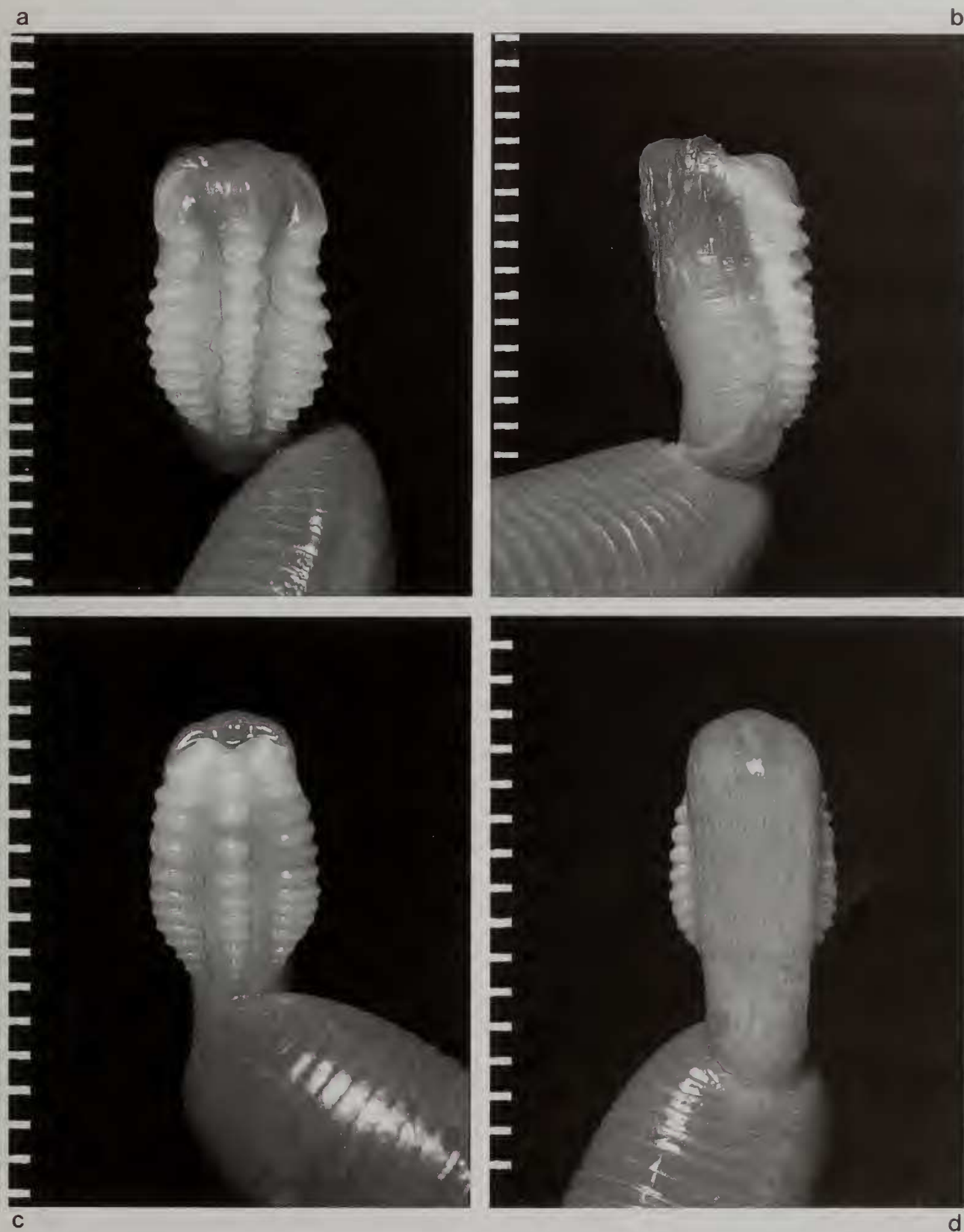


Fig. 10 *Schistometopum gregorii* from Tanzania. Views of (a) dorsal, and (b) right lateral surface of phallus of field specimen MW 3257, and (c) dorsal, and (d) ventral surface of phallus of field specimen MW 3251. Scale bars in mm.

among individuals, but whether this variation is correlated with taxonomy, ontogeny, and/or temporally within any possible reproductive cycles is as yet unknown. Occasionally, minor variations in the ornamentation are seen. For example, the individual shown in Fig. 4 also has a single, poorly formed, transverse thickening ventrally. In the individual shown in Fig. 6, the posteriormost transverse thickening on the right dorsolateral longitudinal ridge extends posterior to the posteriormost transverse thickening on the mid-dorsal longitudinal ridge, whereas the reverse of this pattern (as seen on the left of this individual) is more commonly encountered. Finally, the transverse thickenings or tuberosities are sometimes multipartite.

Figure 9 depicts the phallodeum of an individual identified as *U. cf. oxyurus* (Duméril and Bibron, 1841). Although the precise specific identity of this individual also is not entirely clear, we are confident that it is referable to a species distinct from that (or those) represented in Figs. 4 to 8. For example, the *U. cf. oxyurus* individual comes from a population with substantially more vertebrae (112–115, $n = 18$) than the populations represented by the other figured specimens (93–110, $n > 100$). Despite their apparent specific distinctness, the phallodea of *U. cf. narayani* (Figs. 4 to 8) and *U. cf. oxyurus* (Fig. 9) share the same number and pattern of longitudinal ridges and transverse ornamentation. Thus Wake's (1972: 353) claim that the phallodeal ridges and 'cloacal accessory structures is species-specific' does not appear to hold – at least not at the level of the presence, number, or topographical relations of major features. It might yet hold for morphometric variations of phallodeal features and/or for fine morphological details of the longitudinal ridges and their ornamentation, but this needs further assessment.

That not all species of *Uraeotyphlus* share the same basic phallodeal morphology is revealed by observation of *U. cf. malabaricus* (Beddome, 1870), in which the number and arrangement of longitudinal ridges and their ornamentation is markedly different. Interestingly, analysis of mitochondrial DNA sequence data strongly indicates that *U. narayani* and *U. cf. oxyurus* share a more recent common ancestor with each other than either does with *U. cf. malabaricus* (Gower *et al.*, 2002).

SPECIES' DIFFERENTIATION AND GENERIC IDENTITY. Nussbaum & Pfrender's (1998) recent revision of the caeciliid genus *Schistometopum* recognised two species occurring on opposite sides of the African continent. *S. thomense* (Barboza du Bocage, 1873) is known from São Tomé island in the Gulf of Guinea, and *S. gregorii* (Boulenger, 1894) from lowland coastal regions of Kenya and Tanzania. The validity of the genus has not been seriously questioned, but it is currently diagnosed on a combination of characters, with no known unique synapomorphies.

Wake (1972: 358) described the male cloaca of *S. thomense* as having 'four regularly spaced muscle bands on each side of the cloaca', presumably features of the urodeum, and that 'the posterior part of the cloaca [more the central region, as can be seen when the cloaca is fully dissected] is arranged in three sets of transverse, crescent-shaped muscles, one mid-dorsal, the other two ventrolateral.' Tonutti (1933) described longitudinal phallodeal ridges as dorsal rather than ventrolateral in *S. thomense* and we concur with his assessment (see Fig. 10). Wake found the cloaca of *S. gregorii* to have a similar morphology to that of *S. thomense*. Although we are not convinced that the transverse ridges comprise muscle, we agree that the two species share a similar morphology, and consider the presence of three (though see discussion of *S. gregorii* below) narrow and long longitudinal ridges with a characteristic ornamentation of regularly spaced, scalloped transverse ridges and grooves to be restricted to these two species among material we have

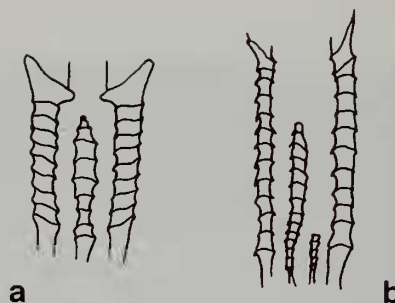


Fig. 11 Sketches showing disposition of major longitudinal ridges and their ornamentation in the dorsal luminal wall of the anterior part of the phallodeum of (a) *Schistometopum thomense* (UMMZ 188027), and (b) *S. gregorii* (UMMZ 147011) from Kenya. Compare with Tanzanian *S. gregorii* shown in Fig. 10. Not drawn to scale.

observed. Thus, this phallodeal structure is potentially a unique diagnostic character of *Schistometopum*.

Wake (1972) considered the phallodeal ridges of *Schistometopum* to resemble the condition in *Geotrypetes*. However, the part of the mid-dorsal longitudinal ridge that bears ornamentation in both *S. thomense* (Fig. 11a) and *S. gregorii* (Figs. 10, 11b) is relatively much longer than the comparable ornamented area in *Geotrypetes seraphini*, which is instead restricted to a small nubbin that lies at, or slightly beyond, the level of the posterior end of the ornamented part of the longitudinal ridges lateral to it (pers. obs. of e.g. UMMZ 172648). In addition, the ornamentation appears to be somewhat different in the two genera, which otherwise also have quite differently organised cloaca (for example, *Schistometopum* lacks blind sacs).

The phallodeum of a single specimen (UMMZ 147011) of *S. gregorii* from Northern Kenya has been examined and a sketch of the ornamented part of the longitudinal ridges is shown in Fig. 11b. The figured morphology is largely similar to that seen in several specimens of *S. thomense* (e.g. Fig. 11a), except that, in UMMZ 147011, there is not a single mid-dorsal ridge, but instead two paramedian longitudinal ridges, one longer than the other. Both of these ridges bear transverse crests, but they are shorter relative to the dorsolateral longitudinal ridges than in the observed specimens of *S. thomense*. The morphology of the mid-dorsal region of the phallodeum in two Tanzanian specimens of *S. gregorii* observed for this study (Fig. 10) both bear a greater resemblance to the condition in *S. thomense* (Fig. 11a) than to the single Kenyan *S. gregorii* (Fig. 11b) examined. The sample size is small, but the observed morphological variation is intriguing in light of Taylor's (1968: 677) suggestion that, based on differences in annulation, the Tanzanian and Kenyan populations of *S. gregorii* might be specifically distinct.

DISCUSSION

The complex structure of the caecilian phallus offers great potential for caecilian systematics, both as a source of diagnostic features for species, and of characters for phylogenetics. However, to fully exploit this potential requires a better understanding of the extent of intraspecific variation that occurs within features that appear to vary interspecifically. Of course, in this regard there is no difference between the caecilian phallus and any other structure employed in systematics, and we suggest that incomplete understanding of variation should temper but not discourage the use of cloacal characters

in caecilian systematics. There is evidence of considerable ontogenetic variation in the development of blind sacs and phallodeal ornamentation, emphasising the need for systematic comparisons to be of co-ordinate developmental stages or of developmental trajectories. There is also evidence of variation in adults in the sizes of the urodeum and phallodeum, and the exact form of ridges, their ornamentation, and other phallodeal structures, at least some of which is seemingly correlated with breeding cycles. Despite Wake's (1998: 183) statement that the morphology of the phallodeum of *Scolecophorus* 'is indeed consistent within the species', the same paper clearly documents intraspecific variation in the number of phallodeal spines in *Scolecophorus uluguruensis* and *S. vittatus* (Boulenger, 1895). Functional considerations lead us to speculate that additional intraspecific variation in phallodeal ornamentation occurs because the phallodeum serves both reproductive and excretory roles. In individuals with well-developed tuberosities, these can interdigitate *in situ* to seemingly obstruct the cloacal lumen. We hypothesise that in these species, at least, cloacal ornamentation would be elaborated at times of courtship but reduced at other times. If correct, differences in reproductive condition would need to be taken into account in any systematic comparisons.

Our observations suggest that the pattern of major longitudinal ridges and often also the number and position of phallodeal tuberosities or other ornamentation is mostly constant within species. The same general pattern occurs in 11 specimens of *Hypogeophis rostratus*, the largest sample of a single species that we have examined in detail. However, detailed study of ontogenetic and population variation is needed to test this constancy and to determine whether variations in the form of phallodeal ornamentation are of systematic utility. Thus, future studies should attempt to increase sample sizes for at least some species. Of the 33 species examined by Wake (1972), her largest sample was 29 specimens of *Gymnophis proxima* (Cope, 1877) whereas sample sizes for the remaining species were low (mean = 1.7), providing little basis for assessing variation. Wake (1972) did not discuss intraspecific variation in any species.

Closely related species (e.g. congeners) tend to have similar cloacal morphologies, providing a strong indication that the cloaca will be a source of stable phylogenetic characters. For example, the absence of a definitive colliculus or any other obvious division of the cloaca into urodeal and phallodeal chambers is a very striking putative synapomorphy of *Dermophis* and *Gymnophis*. These genera have been considered closely related (e.g. Nussbaum & Wilkinson, 1989) but there are no previously reported uniquely derived characters. Similarly, the general form of the longitudinal phallodeal ridges and their ornamentation in *Schistometopum thomense* and *S. gregorii* appears to offer the first known unique diagnostic character for *Schistometopum*. On the other hand, congeners can sometimes be readily distinguished by clear-cut, discrete differences in the patterns of phallodeal ridges and topological relations in their ornamentation.

Contrary to Wake (1972), our investigations of *Uraeotyphlus* suggest that, in at least some cases, cloacal morphology may not be species specific. Instead, it appears that some species that can be clearly differentiated based on traditional morphological characters have a common pattern of phallodeal ridges and ornamentation. Species specific differences in these examples may yet be found in the details of the form of phallodeal morphology, but additional work is needed to test this.

In this survey we have concentrated upon the gross structural features of the caecilian cloaca. The luminal surface of the cloaca appears to be also covered in many minor ridges and grooves (striae). This micro-ornamentation may also yield useful systematic

data but, as with more macroscopic features, studies of this must take into account potential intraspecific variation. In some cases, where we have described major structures as terminating, it might be more accurate to describe them as giving rise to, or being supplanted by, striae. For example, in *Hypogeophis rostratus*, where the main dorsolateral longitudinal ridges and their sulci 'terminate' anteriorly, close to the colliculus, they more accurately continue into inconspicuous striae (MW, pers. obs.). These bend around the lateral margins of the colliculus and open into channels running alongside the main mid-dorsal urodeal ridge. We suspect this arrangement constitutes the passage through which sperm travel from the urodeum to the phallodeum, to be delivered to the female via the dorsolateral sulci that are such a prominent feature of the phallus.

ACKNOWLEDGEMENTS. It is a pleasure to thank our esteemed colleague and friend Garth Underwood for inspiring our research and for enlightening discussions of systematics, cloacae and histology. The assistance in provision of material of too many people to name individually has been indispensable to this work, and is gratefully acknowledged. Thanks to Christian Klug and Claudine Levasseur for assistance with translations, Alex Kupfer for helpful discussions of cloacal form and function, and Harry Taylor for Fig. 10. MW is grateful to Ron Nussbaum for fostering and encouraging his interest in caecilian cloacae, and to David Sever for helpful discussion of amphibian urogenital systems. This paper was improved by critiques from Barry Clarke, Alex Kupfer, Simon Loader and Hendrik Müller and supported in part by NERC grants GST/02/832 and GR/9/2881, and an MRF award.

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